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Factors influencing the local scale colonisation and change in density of a widespread invasive plant species, *Lantana camara*, in South India

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Abstract

Identifying factors that underlie invasive species colonisation and change in density could provide valuable insights into the mechanisms of biological invasions and for invasive species management. We examined a suite of factors potentially influencing the landscape-level invasion of *Lantana camara* L., one of the most ubiquitous invasive species in South Asia. These factors included disturbance factors like forest fires, historical habitat modification, and edge effects, in addition to factors like propagule pressure and habitat suitability. We examined the relative importance of these factors on the colonisation and change in density of *L. camara* in the Biligiri Rangaswamy Temple Tiger Reserve, Western Ghats, India. We used extensive (1997–2008) datasets tracking the presence and abundance of *L. camara* and combined these with corresponding data on disturbances, propagule pressure, and habitat suitability. We used an information-theoretic model selection approach to determine the relative importance of each factor on the colonisation and change in density of *L. camara*. Colonisation was mainly a function of proximity to already established populations (i.e. propagule pressure), whereas increase in *L. camara* density appeared to be constrained by high fire frequency. Research and management efforts need to recognize the multi-dimensional nature of mechanisms underlying *L. camara*'s success during different invasion phases when strategizing interventions to mitigate its effects.

Keywords

Tropical dry forest, disturbance, propagule pressure, forest fire

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Introduction

The likelihood of an introduced species becoming invasive is determined by the interplay of the invader's characteristics (e.g. its high propagule output; Sakai et al. 2001), the abiotic environment (particularly disturbance; Shea and Chesson 2002), and biotic interactions within novel environments (e.g. enemy-release; Keane and Crawley (2002)). The disturbance regime prevalent in an area plays a pivotal role in influencing invasive species success (Davis et al. 2000). Habitats that are subject to natural or anthropogenic disturbances could be particularly vulnerable to invasion (Jauni et al. 2014). In addition to ongoing disturbances, disturbance legacies (e.g., historical clear-cutting), could also make habitats vulnerable to invasion (Seabloom et al. 2003). Lastly, feedback loops between periodic disturbances (like forest fires) and invasive species dominance have been observed in some systems (e.g. the grass-fire cycle; D'Antonio and Vitousek 1992), indicating the pivotal role played by disturbance in biological invasions.

Propagule pressure has also been found to act as an important driver in the invasion process (Rouget and Richardson 2003, von Holle and Simberloff 2005, Lockwood et al. 2005). In an experimental study using forest understory plants, von Holle and Simberloff (2005) found that successful invasions were contingent upon the number of propagules arriving *in situ*, when compared to other factors such as resident diversity and the flooding regime. Propagule pressure, in turn, is dependent upon life history characteristics such as time taken to reach reproductive maturity and dispersal mode – rapidly maturing species with abiotically dispersed seeds tend to be more successful compared to slow-maturing species with biotically dispersed seeds (Daehler 1998).

Both colonisation (i.e. local arrival in a part of the landscape where it was earlier absent), and change in density (i.e. changes in the abundance over time) contributes to invasive plant spread. Change in density influences the probability of maintaining populations in colonised sites and the quantum of propagules released from colonised sites. However, factors that influence colonisation may not necessarily influence density. At the colonisation stage, factors such as proximity to propagule sources may come into play more than factors such as habitat heterogeneity (Rouget and Richardson 2003). Although propagule pressure is largely a function of distance to invasion foci (Rouget and Richardson 2003), proximity to sites of historical or contemporary disturbance may directly determine proximity to propagules. It is therefore necessary to quantify the effects of these factors on invasive plant colonisation, individually, and in tandem.

Change in density, on the other hand, may be determined by the frequency of forest fires or other landscape-level disturbances (Jauni et al. 2014) rather than propagule pressure alone. Although von Holle and Simberloff (2005) experimentally established the primacy of propagule pressure as a determinant of invasions relative to other factors like resident species density and abiotic disturbance (flooding), other studies indicate that disturbance-triggered regeneration favours invasive species over native species (Galatowitsch and Richardson 2005). Given uniform propagule pressure, it could be possible that exploiting windows of opportunity provided by disturbance are key to invasive species success. Although the role of disturbance in the invasion process has

been described in many studies, the specific role of forest fire as a determinant of the spread of invasive species is unclear.

Lantana camara is one of the most globally ubiquitous invasive species (Cronk and Fuller 1995, Day et al. 2003, Vardien et al. 2012). Reports thus far suggest that in some contexts an increase in fire frequency could increase *L. camara* density due to its capacity to readily resprout in response to fire (Hiremath and Sundaram 2005), while in some others, an increase in fire frequency could depress *L. camara* density, possibly by depleting the soil seed bank (Sundaram et al. 2012, Debuse and Lewis 2014).

L. camara was introduced to India a little over two centuries ago, and is today one of the most widespread invasive plant species in the country (Kannan et al. 2013). Based on herbarium records, Kannan et al. (2013) mapped the introduction and spread of *L. camara* across India in the 19th century. Their results show that the spread of *L. camara* in India started in the early 1800s, and accelerated with the development of travel networks and the expansion of colonial forest management thereafter. Yet, while we now have information on temporal and spatial patterns of *L. camara* spread at a national and regional scale, we have so far lacked information on the mechanisms underlying its local scale colonisation and increase in abundance.

We examined factors underpinning the colonisation and change in density of *L. camara* in the Biligiri Rangaswamy Temple Tiger Reserve, a seasonally dry tropical forest landscape in the Western Ghats biodiversity hotspot, India. Rapid *L. camara* invasion has occurred here over the past decade (Sundaram and Hiremath 2012). Given the gaps in our understanding of the *L. camara* invasion process, and the apparent multivariate nature of the factors that influence *L. camara* invasion—and species invasions in general (Gurevitch et al. 2011)—we used an information-theoretic, model-selection approach (Burnham and Anderson 2002) to determine the relative importance of propagule pressure, fire frequency, landscape history, habitat suitability, and contemporary disturbance on the colonisation and change in density of *L. camara*. We expected that colonisation would be driven by propagule pressure while *L. camara* change in density would be driven by disturbance and forest fires.

Methods

Lantana camara L.

Lantana camara (Verbenaceae) is a straggling shrub native to South and Central America. Kannan et al. (2013) document records of multiple introductions of *L. camara* into India beginning from the early 1800s. It was introduced as a garden ornamental because of its attractive – and profuse – flowers, and was also extensively cultivated as a hedge plant. Its abundant sugar rich fruits attract a variety of frugivores, and *L. camara* is dispersed by birds (Bhatt and Kumar 2001) and small mammals (B. Sundaram personal observation). *Lantana camara* is also able to propagate vegetatively by resprouting from rootstock (Day et al. 2003).

Lantana camara started to be mentioned in the literature as invasive about a hundred years after its introduction to India (Tireman 1918, Iyengar 1933). Today, *L. camara* is common in tropical dry forests, slash-and-burn fallows, and pasture-lands all over India (Sharma et al. 2005).

Study area

The Biligiri Rangaswamy Temple Tiger Reserve (hereafter, BRT) in Karnataka, India, where this study was conducted, is part of the Western Ghats biodiversity hotspot (Das et al. 2006). The sanctuary is 540 km^2 in area, and is located between 77°00'–77°16'E, and 11°47'–12°09'N. The terrain is undulating, and elevation ranges from about 600 m in the foothills to about 1800 m in the upper reaches. Annual rainfall in the study area varies along this altitudinal gradient, ranging from ca 900 mm at low elevations to ca 1750 mm at higher elevations. The mean annual temperature is 25.3 °C, but varies with elevation. Winter temperatures drop to a mean minimum of 11 °C at higher elevations, while summer temperatures soar to a mean maximum of 42 °C in the foothills (Murali et al. 1998). Soils are moderately shallow, deep gravelly to sandy clay loams, with parent material classified as inceptisols consisting of granitic gneiss and charnockites (Anon. 1996). The area was declared a Wildlife Sanctuary in 1973 (Barve et al. 2005) and a Tiger Reserve in 2010.

Our study site is an ideal system to examine the mechanisms underlying *L. camara* invasion for two significant reasons. First, spatially explicit data on the presence and abundance of *L. camara* are available for 1997 (Murali and Setty 2001) and 2008 (Sundaram and Hiremath 2012), enabling us to examine the change in *L. camara* distribution and abundance over an 11-year period. Second, we have information on potential factors that may influence colonisation and change in density, which corresponds temporally and spatially with the data on change in *L. camara* distribution and abundance. The study area has a long history of human habitat modification and use. Forestry activities began during the 1930s (Ranganathan 1934) with the establishment of forest blocks to harvest sandalwood (*Santalum album*), bamboos (both *Bambusa arundanacea* and *Dendrocalamus strictus*), and timber (via selection- and clear-felling). In addition to disturbance generated by forestry activities, shifting agriculture was practiced by an indigenous tribe, the Soliga, in several sites across the BRT landscape over centuries, and this entailed the clearing and burning of understory vegetation prior to planting food crops (Madegowda 2009). Early dry-season fires, initiated by the Soliga for landscape management to clear the understory, enable the collection of forest products, and maintain trails, are characteristic of the BRT landscape (Sundaram et al. 2012). Subsequent to BRT being declared a Wildlife Sanctuary, logging (both clear- and selection-felling) and plantation activities were suspended, and most *podus* (Soliga settlements) within the area were relocated to the park's periphery (Fig. 1).

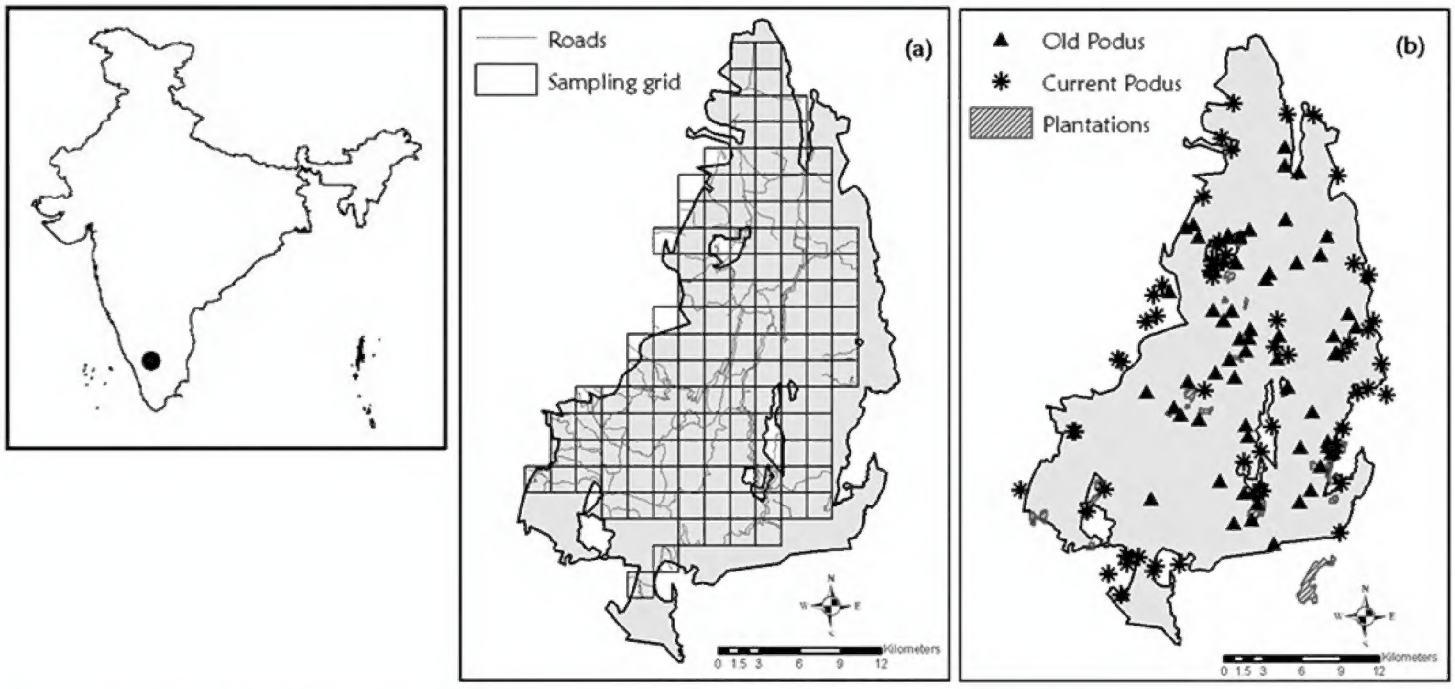

Figure 1. Map of the Biligiri Rangaswamy Temple Tiger Reserve (BRT) showing sampling grids and roads (**a**), old and current podus (Soliga settlements), and areas of historical plantation activity (**b**). Inset map of India shows location of BRT.

There are several forest types in BRT, of which seasonally dry forests constitute approximately 90% of the study area (Krishnaswamy et al. 2009) and include scrub-savanna, dry deciduous, and moist deciduous forests. These forests are extensively invaded by *L. camara* (Sundaram and Hiremath 2012).

Lantana camara colonisation and change in density

Information on *L. camara* distribution in BRT from 1997 came from Murali and Setty (2001), who overlaid a 2 × 2 km grid over the entire study area and established plots at the center of each of the 134 grid cells during January-April 1997; plots were 80 × 5 m in size, with the long axis of plots oriented north-south. They counted and identified all woody stems>1 cm diameter at breast height (dbh) in each plot. Between August 2007 and January 2008, we used the same plot locations and field protocol used by Murali and Setty (2001) to enable assessment of colonisation and change in density since 1997. Twelve of the original 134 plots were found to occur in habitation or plantation during our survey, presumably as a result of a change in land-use at these locations between 1997 and 2008, and data from these plots were excluded.

Spatially explicit data on *L. camara* distribution from 1997 to 2008 enabled us to arrive at our response variables, colonisation and change in density. For examining colonisation between 1997 and 2008, we used the subset of plots that were uninvaded by *L. camara* in 1997 (n = 71). *Lantana camara* change in density between 1997 and 2008 was examined by computing the change in *L. camara* stem density from 1997 to 2008 (stem density in 2008/stem density in 1997). For this we used the subset of plots

that were already invaded by *L. camara* in 1997 (n = 51). Although hypothetically plots may already have attained maximum *L. camara* density in 1997, results from Murali and Setty (2001) suggest low density. The mean density of lantana increased more than three-fold between 1997 and 2008 (Sundaram and Hiremath 2012).

Predictor variables and model parameters

(a) *Lantana camara* neighbourhood index

We developed a *L. camara* neighbourhood index (LNI) assuming that presence of *L. camara* in an adjoining grid cell would contribute to propagule pressure. To calculate LNI in 1997, we used data on *L. camara* presence/absence from Murali and Setty (2001) and scored each grid cell in the study area as 0 (*L. camara* absent) or 1 (*L. camara* present). For each grid cell, the eight adjacent cells were listed and *L. camara* presence/absence scores were then averaged to generate a value of LNI and used as a proxy for propagule pressure exerted on a particular cell. The procedure we used to generate the LNI is admittedly a coarse-scale measure, since we are not taking into account within-grid heterogeneity, but are using only plot data to infer *L. camara* presence/absence across the entire grid cell. It could also be argued that this neighbourhood index is a proxy not just for propagule pressure, but for proximity to habitat suitable for *L. camara*. However, we have assumed that the effect of propagule pressure overrides the effect of habitat suitability in this case, based on findings from previous studies. For example, in their study of the distribution and cover of 3 invasive tree species in South Africa's Agulhas Plains, Rouget and Richardson (2003) found that the intensity of propagule pressure, approximated from the distance to putative invasion foci was a better predictor of invasive species cover than other environmental factors. They also found that population development (in terms of both colonisation and change in density) was driven primarily by propagule pressure; environmental variables came into play only later in the invasion process. That propagule pressure could overwhelm biotic resistance to invasion, and potentially override the effects of disturbance is also suggested by D'Antonio et al. (2001) in the context of plant invasions in California. This occurs because biotic resistance (and disturbance) is variable in space and time, creating windows of opportunity that could be exploited by propagules, if present.

(b) Degree of deciduousness of the canopy

Published information (Day et al. 2003, Sharma et al. 2005, Gentle and Duggin 2006) and observations from our study area suggest that *L. camara* is present in high densities in dry- and moist-deciduous environments compared to wet evergreen environments (Sundaram and Hiremath 2012). Thus, habitat suitability for *L. camara* may be related to canopy deciduousness. An index of '*eco-climatic distance*', a proxy for the degree of

deciduousness (DOD) and green cover, developed for the Western Ghats and BRT by Krishnaswamy et al. (2009), was used because it takes canopy biomass and its intra-annual variability into account. The DOD is a Mahalanobis distance of a pixel to a reference class (in this case, evergreen forest), that uses remotely-sensed, multi-date Normalized Difference Vegetation Index (NDVI) to arrive at a degree of deciduousness for each pixel (Krishnaswamy et al. 2009). Each pixel in the Krishnaswamy et al. (2009) study was 23.5 m × 23.5 m, while the plot size used in this study is 80 m × 5 m. To account for the difference in size between remotely-sensed DOD and plots from which ground data were gathered, values of DOD were averaged for all pixels encompassed within each plot.

Satellite images that were used for the derivation of degree of deciduousness by Krishnaswamy et al. (2009) were from 1998–1999. The density of *L. camara* in BRT was negligible during this period, as we know from the survey carried out just one year prior to this (Murali and Setty 2001). Data from Murali and Setty (2001) indicated that only 2.2% of plots invaded in 1997 had more than 50 lantana stems/plot (Sundaram and Hiremath 2012).

(c) Disturbance

Historical disturbance: Field observations from BRT indicated that a large proportion of historical plantations and agricultural sites are heavily invaded by *L. camara* (B. Sundaram *personal observation*). It is possible that these plantations and habitations were the original source locations from which *L. camara* spread. Historically, plantations of silver oak (*Grevillea* spp.) and teak (*Tectona grandis*) were established in multiple locations. Information about the locations of historical clear- and selection-felling sites was obtained from the field (using a hand-held GPS unit) and from Karnataka Forest Department records (Ranganathan 1934) for the study area. Additionally, locations of historical Soliga habitation sites were obtained from an existing study (Madegowda 2009). The distance from the plot center to the edge of historical plantation and agricultural sites, and from the plot center to the edge of historical Soliga habitation were computed. The lesser of these distances yielded the minimum proximity to historical disturbance (HD).

Contemporary disturbances: Several studies indicate that edge effects (estimated through proximity to habitation, and to roads and streams) may play an important role in *L. camara* invasion (Day et al. 2003, Bradley and Mustard 2006, Raizada et al. 2008). All roads within the study area were mapped using a GPS set to record points every 10 m, while streams were digitized from Survey of India topographical sheets. The minimum perpendicular distance from the plot centre to either roads or streams was calculated to yield a variable called EDGE. The locations of current habitation were recorded in the field using a GPS, digitized, and minimum perpendicular distance in metres between the center of each plot and the habitation boundary was calculated using MapInfo. This yielded a second variable called distance to contemporary disturbance (CD).

Fire frequency (FF): Burnt areas were mapped each year from 1997–2002 (R. Siddappa Setty, unpublished data), and 2004–2007 (this study), yielding fire maps for 10 of the 11 years over which change in *L. camara* distribution has been assessed. Each year during April-May, all motorable roads in BRT were traversed. Visibly burnt areas were marked on a topographical sheet (scale 1:50000, or 1 cm = 500 m). Additional burnt areas that were not visible from the roads were mapped from vantage points within BRT. At least 17 locations across the study area were consistently used as vantage points annually. The topographical sheets on which fires were mapped were scanned and burnt areas were digitized using MapInfo. Based on fire maps from 1997–2002 and 2004–2007 fire frequency was calculated for each grid cell as the total number of times the cell burned between 1997 and 2007. In case the area in a grid cell was incompletely burnt, the grid cell was scored as burnt only if the grid center (where plots were located) was burnt.

After deriving all predictors, we determined the level of correlation (Pearson's r) among predictor variables. We found a significant positive correlation (r = 0.61) between the minimum distance to historical plantation sites and minimum distance to historical habitation sites. Since our final predictor variable for historical disturbance (HD) was derived from the lesser of the two distances to historical plantation sites or historical habitation sites, this correlation would not affect our model selection exercise. None of the other predictors (or their components) were correlated.

Statistical analyses

Analyses were performed separately on data subsets corresponding to colonisation and change in density. An information-theoretic, model-selection approach (Burnham and Anderson 2002) was adopted to evaluate suitability of various predictors to describe the two response variables—colonisation and change in density. Rather than employing conventional hypothesis testing approaches, we used a model-selection approach in order to identify the relative importance of several predictors of *L. camara* invasion, both individually and synergistically.

After response and predictor variables were derived, candidate sets of models (global model with all predictors, single predictor models, and models containing predictor pairs) were developed *a priori* to examine factors driving colonisation and change in density. For both candidate sets, the explanatory variables used were identical, and in each candidate set of models, all predictor variables were used an equal number of times. Having a balanced model set was vital for the purposes of calculating the importance of each predictor variable individually (Burnham and Anderson 2002, Doherty et al. 2012). The predictor variables used in both candidate sets of models were (a) fire frequency (FF), (b) degree of deciduousness (DOD), (c) minimum distance to historical disturbance (either plantations or habitation; HD), (d) minimum distance to contemporary disturbance (existing habitation; CD), (e) minimum distance to edge (either roads or streams; EDGE), and lastly, (f) *L. camara* neighbourhood index (LNI).

Both candidate sets (one each for colonisation and change in density) contained a global model that included all predictors. The global models of colonisation and change in density included only two-way interactions (e.g., FF:EDGE) between predictors. Three-, four- and five-way interactions could not be included on account of small sample sizes. After defining the global model in each candidate set, a subset of separate single-predictor models was then added (a total of six models, one for each predictor). Finally, a subset of separate two-way additive models containing all unique combinations of predictor variables was added (a total of 15 models). Thus each candidate set had a total of 22 models (1 global model + 6 single predictor models + 15 two-way additive models).

A generalized linear model (GLM) with binomial errors and a logit link was used to model colonisation. For modeling *L. camara* change in density, a GLM with Gaussian errors and a log link was used. To account for instances where the density of *L. camara* in 2008 was 0 (a total of seven cases), we added a miniscule number (0.001), so that the log value of 2008 density/1997 density could be calculated.

For both candidate sets of models, a set of background tests were conducted before progressing to the model-selection stage (Burnham and Anderson 2002). The fit of the global model (% variance explained) was first examined. The data were then checked for overdispersion (i.e., if the sampling variance exceeded the theoretical (model-based) variance in the global model; Burnham and Anderson 2002). There was no evidence of overdispersion in either colonisation ($\hat{c}$ = 0.12) or change in density data ($\hat{c}$ = 0.43). After checking for overdispersion, Akaike's Information Criterion, corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) was calculated for each model. By including a bias correction term for complexity and small sample sizes, AIC_c estimates provide a maximum-likelihood based parsimonious measure of model fit. For each model in a candidate set, Δ_i (the value of AIC_c in the i^{th} model – minimum value of AIC_c occurring within the candidate model set) was calculated (Burnham and Anderson 2002). Based on Δ_i values, Akaike weights (relative likelihood of a focal model versus all hypothesized models) were calculated (Burnham and Anderson 2002). Lastly, by summing the Akaike weights for all models where a particular predictor appears, the "weight of evidence of support" (e.g., Marchetti et al. 2004) for each predictor was calculated across all models within a candidate set. Data analysis was conducted using R version 2.9.0. (R Development Core Team 2009).

Results

Lantana camara colonisation

The probability of colonisation increased with an increase in the *L. camara* neighbourhood index around each plot in 1997 (Fig. 2a). The model that used only the *L. camara* neighbourhood index as a predictor of colonisation had the lowest AIC_c value and the highest Akaike weight when compared to all other models (Table 1). Although the *L.*

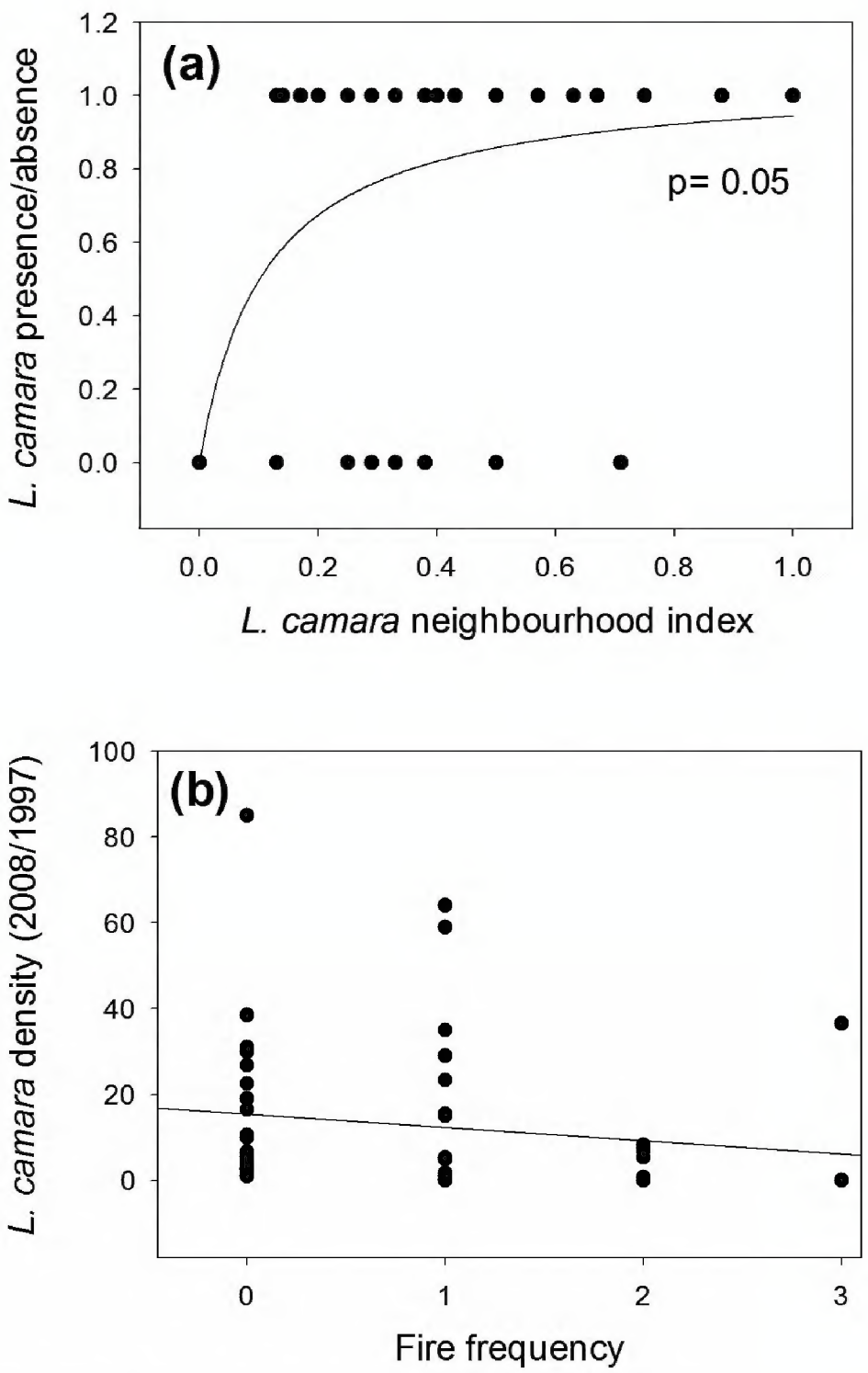

Figure 2. Variables that best explain *L. camara* colonisation (**a**), and change in *L. camara* density (**b**). P-values are taken from single-predictor GLM analyses.

camara neighbourhood index explained only 6.2% of the deviance from the intercept-only model for colonisation data, parameter averaging indicated that the *L. camara* neighbourhood index had the highest evidence of support as a predictor of colonisation when compared to all other covariates (Table 3). The value of the *L. camara* neighbourhood index around 71 plots uninvaded in 1997 varied from 0 (*L. camara* free neighbourhood) to 1 (completely *L. camara* invaded neighbourhood), with an average the *L. camara* neighbourhood index of 0.38 ± 0.021. By 2008, a large majority of these plots (54/71 = 76%) were invaded by *L. camara*.

Other disturbance factors that affect the study area, such as fire frequency and proximity to edge, did not emerge as being important for explaining *L. camara*

Table 1. Models to explain *Lantana camara* colonisation with their corresponding AIC_c (corrected AIC), Δ_i (value of AIC_c in the i^{th} model – minimum value of AIC_c), Akaike weights and percent deviance explained. The single-predictor model explaining the maximum deviance is in bold typeface.

Model	AIC_c	Δ_i	Akaike weights	% deviance explained
L. camara colonisation (n= 71)				
Global	116.05	38.27	0.000	51.12
Fire frequency (FF)	81.70	3.92	0.047	< 1
Degree of deciduousness (DOD)	82.19	4.41	0.036	< 1
Proximity to historical disturbance (HD)	82.04	4.26	0.039	< 1
Proximity to contemporary disturbance (CD)	82.26	4.48	0.035	< 1
Proximity to edge (EDGE)	82.42	4.64	0.032	< 1
***L. camara* neighbourhood index (LNI)**	**77.78**	**0.00**	**0.330**	**6.19**
FF:DOD	84.39	6.61	0.012	1.60
FF:HD	84.56	6.78	0.011	1.34
FF:CD	84.61	6.83	0.011	1.27
FF:EDGE	84.82	7.04	0.010	< 1
DOD:HD	84.30	6.52	0.013	1.69
DOD:CD	85.13	7.36	0.008	< 1
DOD:EDGE	85.27	7.49	0.008	< 1
HD:CD	85.04	7.26	0.009	< 1
HD:EDGE	85.16	7.39	0.008	< 1
CD:EDGE	85.36	7.59	0.007	< 1
LNI:FF	80.44	2.66	0.087	6.81
LNI:DOD	80.68	2.90	0.077	6.50
LNI:HD	79.96	2.18	0.111	7.45
LNI:CD	80.02	2.24	0.108	7.38
LNI:EDGE	123.41	45.63	0.000	7.24

colonisation when compared to the *L. camara* neighbourhood index alone. The global model (all predictors individually, and all two-way additive interactions of predictors) explained 51.1% of the deviance from the intercept-only model.

Lantana camara change in density

The spatial extent of *L. camara* in BRT increased dramatically from 1997 to 2008. *Lantana camara* was present in 41% of plots across the 540 km^2 of BRT in 1997 (Murali and Setty 2001), but had spread to 81% of plots by 2008; this doubling in spatial extent was accompanied by a more than 3-fold increase in density (Sundaram and Hiremath 2012). Of the total 51 plots that were invaded in 1997, *L. camara* density increased in 37 plots, remained the same in 2 plots, and decreased in 12 plots.

The global model containing all predictors and their interactions explained 56.8% of the deviance from the intercept-only model for *L. camara* density data. The

Table 2. Models to explain *Lantana camara* change in density with their corresponding AIC_c (corrected AIC), Δ_i (value of AICc in the i^{th} model – minimum value of AICc), Akaike weights and percent deviance explained. The single-predictor model explaining the maximum deviance is in bold typeface.

Model	AIC_c	Δ_i	Akaike weights	% deviance explained
L. camara density (n=51)				
Global	219.71	50.76	0.000	56.75
Fire frequency (FF)	**168.94**	**0.00**	**0.400**	**23.59**
Degree of deciduousness (DOD)	182.67	13.72	0.000	< 1
Proximity to historical disturbance (HD)	182.51	13.57	0.000	< 1
Proximity to contemporary disturbance (CD)	182.64	13.70	0.000	< 1
Proximity to edge (EDGE)	181.98	13.03	0.001	1.35
L. camara neighbourhood index (LNI)	182.36	13.42	0.000	< 1
FF:DOD	172.12	3.17	0.083	23.69
FF:HD	171.27	2.32	0.127	24.95
FF:CD	172.15	3.20	0.082	23.65
FF:EDGE	170.31	1.37	0.204	26.35
DOD:HD	185.69	16.74	0.000	< 1
DOD:CD	185.87	16.93	0.000	< 1
DOD:EDGE	185.18	16.24	0.000	1.41
HD:CD	185.71	16.77	0.000	< 1
HD:EDGE	185.11	16.16	0.000	1.56
CD:EDGE	185.21	16.27	0.000	1.36
LNI:FF	171.74	2.79	0.100	24.26
LNI:DOD	185.60	16.65	0.000	< 1
LNI:HD	185.27	16.32	0.000	1.25
LNI:CD	185.57	16.63	0.000	< 1
LNI:EDGE	184.94	16.00	0.000	1.88

Table 3. Weight of evidence in favour of each variable for explaining *L. camara* colonisation and change in density. The weights for each variable were calculated by summing the Akaike weights of all models where the predictor variable of interest appears (Burnham and Anderson 2002). Greater weights (highlighted) are indicative of the most important predictor, relative to all others.

Predictor variables	Colonisation	Change in density
Fire frequency	0.12	**0.62**
Degree of deciduousness	0.10	0.05
Proximity to historical disturbance	0.13	0.08
Proximity to contemporary disturbance	0.12	0.05
Proximity to edge	0.04	0.13
L. camara neighbourhood index	**0.48**	0.06

frequency of fire in each grid cell during 1997–2008 emerged as the best predictor of change in *L. camara* density and explained 23.6% of the deviance from the intercept-only model for the data (Table 2). Between 1997 and 2008, 22 plots were

unburned, 19 plots had one instance of fire, 6 plots had two instances of fire, and 4 plots had three instances of fire. Contrary to expectation, change in *L. camara* density and fire frequency appeared to be negatively related. An increase in fire frequency was accompanied by a decrease, rather than an increase in *L. camara* density. Fire frequency and change in *L. camara* density appeared to be negatively related, although we have very few plots that burned more than two times to be able to assert this trend as definitive (Fig. 2b). Summing the Akaike weights across all models where fire frequency appeared as a predictor revealed that fire frequency had the highest evidence of support when compared to all other predictors (Table 3). Although there was a positive relationship between edge and change in *L. camara* density, edge was a distant second to fire frequency in terms of the percent deviance explained (Table 2). The weight of evidence in favour of edge was also low compared with that of fire frequency (Table 3).

Discussion

Results from this study indicate that the factors that are important for *L. camara* invasion differ across stages. Propagule pressure (as inferred from the *L. camara* neighbourhood index) plays an important role in increasing the probability of local colonization of *L. camara*. Following *L. camara* colonisation, fire appears to limit *L. camara* density. While two factors have emerged as being important mechanisms of the *L. camara* invasion process, the three other disturbance factors taken into account in this study (distance to historical disturbance, distance to current human habitation, and distance to edge) and *L. camara* habitat suitability, also play a role. The absence of interactions among our predictor variables was surprising, given our initial expectation of synergistic interaction effects between predictors.

In addition to the factors identified by this study as potential underlying mechanisms of *L. camara* colonisation and change in density, contemporary reports of *L. camara* proliferation in the larger Western Ghats landscape, e.g., in nearby protected areas like Bandipur (Prasad 2010) and Mudumalai (Ramaswami et al. 2014) indicate the possible role of other mechanisms operating at a larger scale, e.g., extended drought or stochastic rainfall. Additionally, the effect of other local-scale factors e.g., biotic interactions, soil, and topography, as possible mechanisms underlying invasion have not been investigated by this study.

Lantana camara colonisation and the importance of the *L. camara* neighbourhood index

In BRT, *L. camara* produces large fruit crops, sometimes up to ten thousand fruits per plant over a single fruiting season (Monika Kaushik, unpublished data). It is likely that arrival of *L. camara* propagules is enhanced by the year-round fruiting of

the species combined with the lack of dispersal limitation. Indeed, studies on the Island of Reunion have shown that larger populations of dispersers (e.g., the invasive red-whiskered bulbul) are supported in areas invaded by four bird-dispersed invasive plants that produce seeds year-round (including *L. camara*) compared to areas with a low invasive plant density. This suggests a positive feedback between presence of propagules and presence of dispersers (Mandon-Dalger et al. 2004). Bulbuls are responsible for the dispersal of *L. camara* seeds in India as well, with *L. camara* fruits forming up to 10% of their diet (Bhatt and Kumar 2001). Studies from Hong Kong show that *L. camara*'s sugar-rich berries also attract other birds (e.g., light-vented bulbul; Corlett 1998). Preliminary studies from our site show that frugivorous bird density and diversity is higher in areas with high lantana fruit density, indicating that birds could be important dispersers of *L. camara* fruits in these forests as well (Monika Kaushik, unpublished).

In addition to its dispersal by frugivorous birds, we have observed *L. camara* seeds in feces of wild pigs and sloth bears in BRT, although there are no published records of *L. camara* seed dispersal by mammals. In addition to sexual modes of propagation, it should also be noted that *L. camara* propagates vegetatively through rootstock (Day et al. 2003), implying that the non-detection of stems aboveground does not necessarily imply the absence of *L. camara* in a given site as rootstock may regenerate when favourable conditions (e.g., a rainfall event) occurs.

While the *L. camara* neighbourhood index emerged as the primary driver of *L. camara* colonisation, other predictors were not negligible, nor sizeable, and the global model explained 51.1% of the variance in the data. The effects of predictors associated with disturbance, such as distance to edge, fire frequency, and distance to both contemporary and historical disturbance, were almost similar. Both Daehler (1998) and Colautti et al. (2006) observe that synergy between factors that influence both the invasiveness of species and the invasibility of landscapes is the rule, rather than the exception. Although this points to a synergy between factors that promote invasiveness (propagule pressure, or rather the *L. camara* neighbourhood index, in this case) and ecosystem invasibility (fire frequency, disturbance and edge), we were unable to detect interactions between predictor pairs.

On the other hand, the relatively lower weight of evidence in favour of degree of deciduousness when compared to the *L. camara* neighbourhood index (and also edge and fire frequency) may be related to the relative representation of different forest types within the BRT landscape. Although a large proportion of our study area is deciduous (~90%; Krishnaswamy et al. 2009) the degree of deciduousness is a continuous variable that spans the continuum in phenological and tree density variation across different types of tropical deciduous forest and savanna-woodland vegetation types (Krishnaswamy et al. 2009, Krishnaswamy 2013). We thus expected that degree of deciduousness would be a good predictor of *L. camara* colonisation, since *L. camara* is known to be sensitive to moisture availability and canopy openness (Sharma et al. 2005). However, it could be that the scale at which the degree of deciduousness was calculated differs from the scale at which *L. camara* colonises habitat.

Fire as a factor limiting *L. camara* change in density

Results from our study have improved our understanding of the relationship between *L. camara* and fire. Some conceptual models of *L. camara* invasibility have hypothesized that an increase in fire frequency could potentially favour *L. camara* (Hiremath and Sundaram 2005, Sharma et al. 2005). More recent work (Sundaram et al. 2012, this study) suggests the opposite, that *L. camara* density may be depressed by fire. Our results are consistent with observed fire effects on *L. camara* in Australia (Day et al. 2003, Debuse and Lewis 2014), i.e., that frequent fires prevent, rather than encourage, *L. camara* spread. We also have evidence to suggest that fires may reduce the density of viable *L. camara* seeds in the soil seed bank (Hiremath and Sundaram 2013).

Just as the role of fire in limiting *L. camara* density was contrary to our expectations, so too was the minimal role of degree of deciduousness and the *L. camara* neighbourhood index in influencing *L. camara* density. Studies from Australia and Africa show that *L. camara* change in density is enhanced by the presence of open canopies or gaps (Totland et al. 2005). In our case, the effects of degree of deciduousness are probably masked by the large spatial extent of deciduous forests in BRT compared to other forest types.

Propagule pressure – as inferred from the *L. camara* neighbourhood index in this case – presumably does not play much of a role in influencing *L. camara* density because allochthonous dispersal (i.e., arrival of seeds from outside) may cease to be important following the colonisation of *L. camara* at a site. Given the young age to maturity of *L. camara* and the large numbers of fruits produced per individual, resulting autochthonous seed arrival (i.e., seeds produced on-site) may swamp the effects of seeds arriving from elsewhere.

Suppression of forest fires and windows of opportunity for *L. camara* invasion

Davis et al. (2000) point out the complex nature of the invasion process resulting from its dependence on intermittent disturbance. Additionally, these disturbances must coincide with propagule availability in order to increase the possibility of successful invasion. In the case of *L. camara*, change in the disturbance regime caused by the suppression of forest fires has probably increased invasibility of some ecosystems (Sundaram et al. 2012) with propagule pressure exerted by the soil seed bank (Hiremath and Sundaram 2013, Debuse and Lewis 2014) as the causal mechanistic link. Ecosystem susceptibility to invasion is therefore not a static or permanent attribute, but one that fluctuates over time depending on favourable conditions being created (Davis et al. 2000), and contingent on propagule pressure being present to make use of windows of opportunity.

In Australia and in India, *L. camara* invasion is probably driven by the capacity of propagule pressure to overwhelm ecological resistance to invasion. D'Antonio et al. (2001) decompose ecological resistance into abiotic (climate conditions, soil

characteristics) and biotic (competition, parasitism, pathogen attack) components and further suggest that when ecological resistance to invasion is high (for example, in areas where fires are a regular occurrence), invasion would occur only when propagule pressure is high, or when invaders themselves can alter resistance. Similar to Davis et al. (2000), D'Antonio et al. (2001) also theorize that high ecological resistance to invasion could be overwhelmed by low, but steady, supply of propagules in space and time, allowing for the exploitation of windows of opportunity.

Management implications

Lantana camara invasion in BRT is the product of a complex interplay between propagule pressure and frequency of forest fires. Clearly, therefore, land managers and biologists need to take into account the inherent multivariate nature of *L. camara* invasion when coordinating eradication or control activities.

Once a species is established, the reduction of propagule pressure is a challenging task (Lockwood et al. 2005). Limiting propagule pressure by physical removal of *L. camara* has been found to be successful, e.g., in Australia (Day et al. 2003) and South Africa (van Wilgen et al. 2004), although costs of removal are prohibitive when the area of operation is large. Additionally, *L. camara* removal has to be conducted repeatedly because of *L. camara* re-growth (Day et al. 2003, Babu et al. 2009, Ramaswami et al. 2014). Prioritizing *L. camara* removal activities in heavily invaded areas could help reduce propagule pressure in the long run (Chornesky et al. 2005), provided *L. camara* colonisation and density are contained in areas that are currently less invaded.

In addition to propagule pressure, our finding that fire limits *L. camara* density also has important management implications. In the Indian context, fires have been regarded by forest managers as uniformly detrimental (Bahuguna and Upadhyay 2002). However, *L. camara* control efforts elsewhere have successfully used fire as a cheap and effective management tool (Day et al. 2003, Debuse and Lewis 2014). On a cautionary note, the use of fire could cause undesirable damage to native trees and other biodiversity components due to abundant fuel provided by *L. camara*. However, using regulated fire as a management tool could be considered if *L. camara* abundance and density could be first reduced by physical removal. Forest managers have attempted physical removals of *L. camara*, but without repeated removals over large areas, removal efforts have largely failed (Sundaram et al. 2012). *Lantana camara* control through fire may be more feasible in deciduous forests, assuming fuel loads could be lowered and kept low.

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